PAN-PACIFIC ENTOMOLOGIST
76(1): 1–11, (2000)

THE AUSTRALIAN FRUIT FLY PARASITOID *DIACHASMIMORPHA KRAUSSII* (FULLAWAY): LIFE HISTORY, OVIPOSITIONAL PATTERNS, DISTRIBUTION AND HOSTS (HYMENOPTERA: BRACONIDAE: OPIINAE)

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Abstract.—*Diachasmimorpha kraussii* is a larval-pupal parasitoid of tephritid fruit flies in Australia. It is currently being considered for release against fruit fly pests in Hawaii. Virgin *D. kraussii* females lived longer (mean = 31.4 days; n = 10) than mated females (mean = 27.6 days; n = 10) by a factor of about 12%. The rate of offspring production per day by virgins (about four emerging adults per day) was the same as that of mated females, so virgins tended to produce more offspring in total (mean = 125) than did mated females (mean = 112), but the difference was not statistically significant. The time between egg deposition and emergence of the resultant adult varied from 16 days to more than 300 days, and males achieved maximum emergence before females. Adult wasps emerged at any time of the photophase, both under laboratory and field conditions, but the rate declined towards the end of the daylight period. Adult females oviposited more actively during the day than at night (30.8 vs 19 adults), and the pattern tended to be stronger when wasps were exposed to hosts initially during the scotophase (37.4 vs 18.4 adults). Mated females produced female-biased brood sex ratios of about 0.28 (proportion of males) on average, and the older the mother wasps the greater the proportion of female offspring produced. *Diachasmimorpha kraussii* is distributed only in northern and eastern Australia, as far south as New South Wales. It has been recorded from 13 host fly species and in association with 18 host plant species.

Key Words.—Insecta, *Diachasmimorpha kraussii*, parasitoid, Braconidae, Tephritidae, oviposition, fecundity, sex ratio, delayed emergence, distribution, hosts.

Braconid parasitoids are the major natural enemies of tephritid fruit flies and have been used for biological control in various parts of the world. Although several species have been used in this capacity, fewer than a dozen are relatively well known, e.g., *Diachasmimorpha longicaudata* (Ashmead), *D. tryoni* (Cameron), *Fopius arisanus* (Sonan), *F. vandenboschi* (Fullaway) and *Psyttalia fletcheri* (Silvestri) (Willard 1920; Leyva et al. 1991; Ramadan et al., 1991, 1992, 1994a, b; Messing & Jang 1992; Messing et al. 1996; Purcell 1998). Little information is available about the other species, and for some not even basic information on life history has been published. This is the case with the Australian species *D. kraussii*, despite it having been described almost 50 years ago (Fullaway 1951), when it was used in biological control efforts. *Diachasmimorpha kraussii* was introduced into Hawaii between 1947 and 1952, cultured on *Ceratitis capitata* Wiedemann and released in areas infested with this pest species. It did not establish permanently (Clausen et al. 1965), but the species is currently being cultured and considered for further releases against *C. capitata* (R. Messing, personal communication). The hosts recorded for *D. kraussii* to date include *Bactrocera barringtoniae* (Tryon), *B. cacuminata* (Hering), *B. dorsalis* (Hendel), *B. jar-*

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visi (Tryon), *B. kraussii* (Hardy), *B. murrayi* (Perkins) and *B. pallida* (Perkins & May) (Clausen et al. 1965). Recent results show, however, that *D. kraussii* cannot develop successfully in Hawaiian *B. dorsalis* flies (R. Messing, personal communication).

To facilitate the use of *D. kraussii* in biological control, we investigated several aspects of its biology and ecology, namely: (i) adult life span and fecundity, (ii) diurnal and nocturnal levels of oviposition and (iii) developmental duration and emergence patterns. The Australian distribution, host flies and host plants of *D. kraussii* were evaluated from museum specimens and from personal collections.

Materials and Methods

Insect Cultures.—A *Bactrocera tryoni* (Froggatt) culture was initiated from a colony held at the Queensland Department of Primary Industries, Long Pocket, Brisbane. We used the culture technique described by Heather & Corcoran (1985), except for providing Vegemite® (concentrated yeast extract) as a protein source for adult flies, instead of protein hydrolysate.

The *D. kraussii* colony was started with about 35 pairs reared from *B. tryoni* puparia derived from Brazilian cherries (*Eugenia uniflora* L.) collected in St Lucia, Brisbane, in November 1990. The adult *D. kraussii* were exposed, in a 15 × 15 × 30 cm perspex cage, to 3rd instar (eight days old since oviposition) fruit fly larvae that were restrained in an "oviposition unit" (see below). Honey was always available to adult wasps, both in culture and in all experiments. Hosts and parasitoids were reared at 25 ± 1° C, 60 ± 5% R.H. and 12:12 L:D. Experiments were also conducted under these conditions.

"Oviposition units" were prepared from a 7.5 cm diameter plastic lid with a raised outer rim (0.6 cm high). The inside cavity of the lid was filled with larval medium into which the *B. tryoni* larvae had been placed. The whole unit was wrapped with tightly-stretched Parafilm®, through which the wasps readily oviposited.

For culturing purposes, oviposition units were exposed to *D. kraussii* adults for 24 h. Units were then unwrapped and placed in a 1000 ml plastic container lined with sawdust. No additional larval medium was needed because the fruit flies always pupated within 24 h of their removal from the oviposition cage. An excess of larval medium, which would encourage fungal growth, was thus avoided. Fungi, if present, made it difficult for fruit fly larvae to spring into the sawdust to pupate. The puparia were sieved from the sawdust and held in a 30 ml plastic cup for adult emergence.

Life Span, Developmental Duration and Reproductive Capacity.—Ten *D. kraussii* females, three days old, were exposed to conspecific males, one day old, for mating (one pair/mating unit (Rungrojwanich & Walter 1999)). After each female had mated (all mated within 10 min), she was held alone in an inverted 125 ml plastic container and exposed to hosts (i.e., early on the fourth day after eclosion). Each container had a 3 cm diameter hole in the bottom with fine muslin glued over it. The containers were kept upside down so that the lids could serve as oviposition units. Each oviposition unit contained 20 *B. tryoni* larvae. After each 24 h of exposure, the oviposition unit was replaced and the old one transferred to its own 1000 ml plastic container for pupation of the larvae. The life span of each wasp was monitored.

The pupae were sieved and placed in a 30 ml plastic cup for emergence. Each plastic cup was cross-labelled to its adult female and day of exposure. Pupae in each plastic cup were checked daily for emergence over 12 months, to establish the minimum fecundity of each female and the duration between oviposition and adult emergence. Emerged wasps were sexed and counted.

The above procedures were followed at the same time, using 10 virgin *D. kraussii* females (three days old) for comparative purposes. Ten oviposition units (20 *B. tryoni* larvae/unit) were also prepared daily as a control, to check the survival rate of unparasitized *B. tryoni*.

Diel Patterns of Emergence and Ovipositional Activity.—To determine the diel pattern of *D. kraussii* emergence, a set of parasitized *B. tryoni* puparia, on the verge of eclosing, were placed in a 250 ml plastic container. At the anticipated time of peak emergence, the puparia were checked hourly through three consecutive days and the number and sex of *D. kraussii* that emerged each hour was recorded. Preliminary tests had shown no emergence during the scotophase.

To check emergence patterns in the field, laboratory-parasitized *B. tryoni* puparia (prepared as above) were held in 30 ml plastic cups (about 50 puparia/cup) each of which was placed on the bottom of a 1000 ml plastic container. The lid of each large container was cut to allow another 30 ml plastic "catching" cup to be inserted through the hole, inverted, so its base protruded to the outside. The large outer containers were covered with aluminium foil to reflect light. Only the 30 ml plastic "catching" cups received light, to which the *D. kraussii* adults were attracted. The apparatus was placed in the shade of a Brazilian cherry tree at St Lucia, Brisbane, on 2 Feb 1993 at 23:00 h and removed three days later at 20:00 h. The "catching" cups were checked hourly between 04:30 h and 18:30 h and the *D. kraussii* that had emerged were removed, sexed and counted.

To assess the influence of day and night conditions on levels of ovipositional behaviour, 15 *D. kraussii* females, three days old, were each exposed to a different conspecific male, one day old, for mating (one pair/mating unit). After mating, females were transferred to perspex cages (five females/10 × 10 × 15 cm cage). An oviposition unit (100 *B. tryoni* larvae/unit) was placed in each cage for the light period 07:00 h to 17:00 h and another was substituted between 19:00 h and 05:00 h (dark period), in a constant environment room (conditions above). The procedure was repeated with new oviposition units for three consecutive photophases and scotophases. After exposure, each oviposition unit was transferred to its own 1000 ml plastic container to await pupation of the flies. The numbers of *B. tryoni* and *D. kraussii* adults that resulted from oviposition during the light and dark exposures were sexed and counted.

To establish whether mated females that had never oviposited during the photophase would oviposit during the scotophase, a 2nd test was conducted following the above procedures, but the times of exposure were reversed i.e., wasps were initially exposed from 19:00 h to 05:00 h and only after that between 07:00 h to 17:00 h.

Results and Discussion

Life Span, Developmental Duration and Reproductive Capacity.—The mean lifetime production of adult offspring by mated *D. kraussii* females (± SE) was 111.7 (± 11.29, $n = 10$), and was not significantly different ($t = -0.85$, $P =$

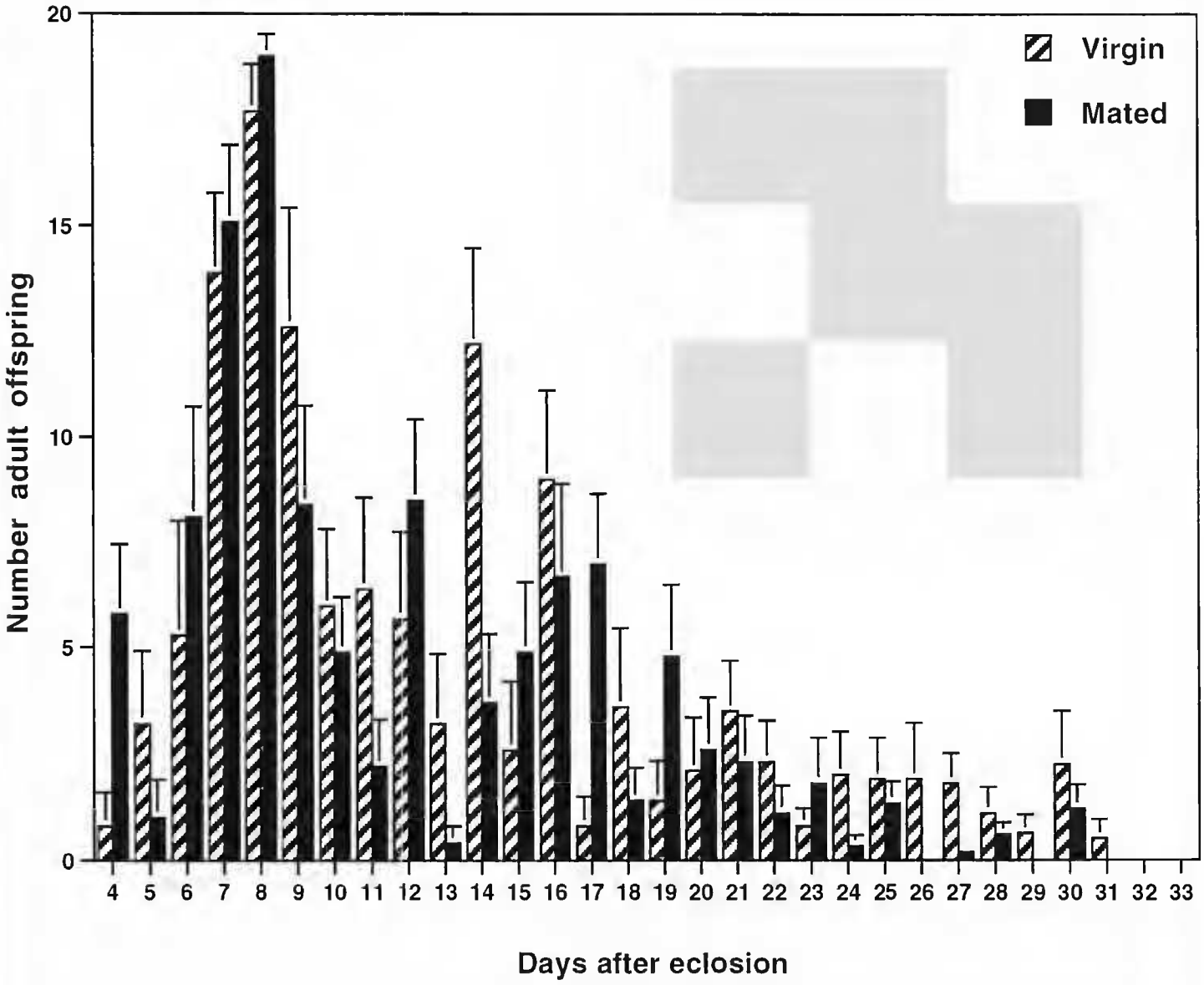

Figure 1. Number of offspring produced by virgin and mated *Diachasmimorpha kraussii* females during each day of their lives. Their first day of exposure to hosts was their 4th day after eclosion. The number ($\bar{x} \pm$ SE) of adults that emerged from the eggs deposited each day of exposure is given. Ten replicates were run, but that dropped in the virgin treatment to 9 (day 30), 8 (d 31), 7 (d 33), 5 (d 34) and none were alive on day 35. The equivalent data for mated females is 8 (d 25), 7 (d 27), 6 (d 32), 3 (d 34) and 0 on day 35.

0.4141) from that of virgins (124.5 ($\pm$ 10.34, n = 10)). Although mated females had a life span (27.6 $\pm$ 4.55 days) significantly shorter than that of virgins (31.4 $\pm$ 1.96 days) (Wilcoxon two-sample test t = 0.0742, P = 0.0315), the mated females produced more adult offspring per day (4.19 $\pm$ 0.51, n = 10) than did virgin females (3.97 $\pm$ 0.33, n = 10) (Wilcoxon two-sample test t = 0.0514, P = 0.0376). Offspring production peaked early (mean of 15–20/d on days 7–8 of adult life), declined abruptly but somewhat erratically to steady low levels (3/day or less) by day 20, and ceased on the last few days of adult life (Fig. 1).

The mean ($\pm$ SE) number of dead fruit fly puparia in the controls (10.7 $\pm$ 0.48) was not significantly different from the number dying (without yielding a parasitoid) after exposure to mated (11.2 $\pm$ 0.56) or virgin (11.1 $\pm$ 0.27) females (Kruskal-Wallis χ^2 = 0.96086, P = 0.6185, df = 2). Thus, ovipositor probing by the wasps probably was not responsible for additional mortality.

Male offspring started to emerge (and achieved the maximum rate of emergence per day) one day before their female siblings (Table 1). The male offspring produced by virgin females achieved maximum emergence on the same day as the

Table 1. Duration until first emergence and maximum rate of emergence (days since parasitoid oviposition) of offspring of mated (MF) and virgin females (VF) of *Diachasmimorpha kraussii*. The number of offspring that emerged during the relevant time period is given in brackets. The number of days taken to achieve 50%, 75% and 100% cumulative emergence is given.

Parent	Offspring sex	Day of		Cumulative emergence (days)		
		First emergence	Maximum emergence	50%	75%	100%
VF	m	16 (1)	19 (408)	19	25	335
MF	m	18 (10)	19 (53)	50	135	335
MF	f	19 (3)	22 (122)	25	63	297

male offspring of mated females, but their first emergence was two days sooner (Table 1). The overall emergence pattern (Fig. 2) of the male offspring produced by mated females was not significantly different from that of their sisters (Kolmogorov-Smirnov two-sample test, $D_{(332,785)} = 0.037$, $\chi^2 = 1.278$, $P > 0.05$), but

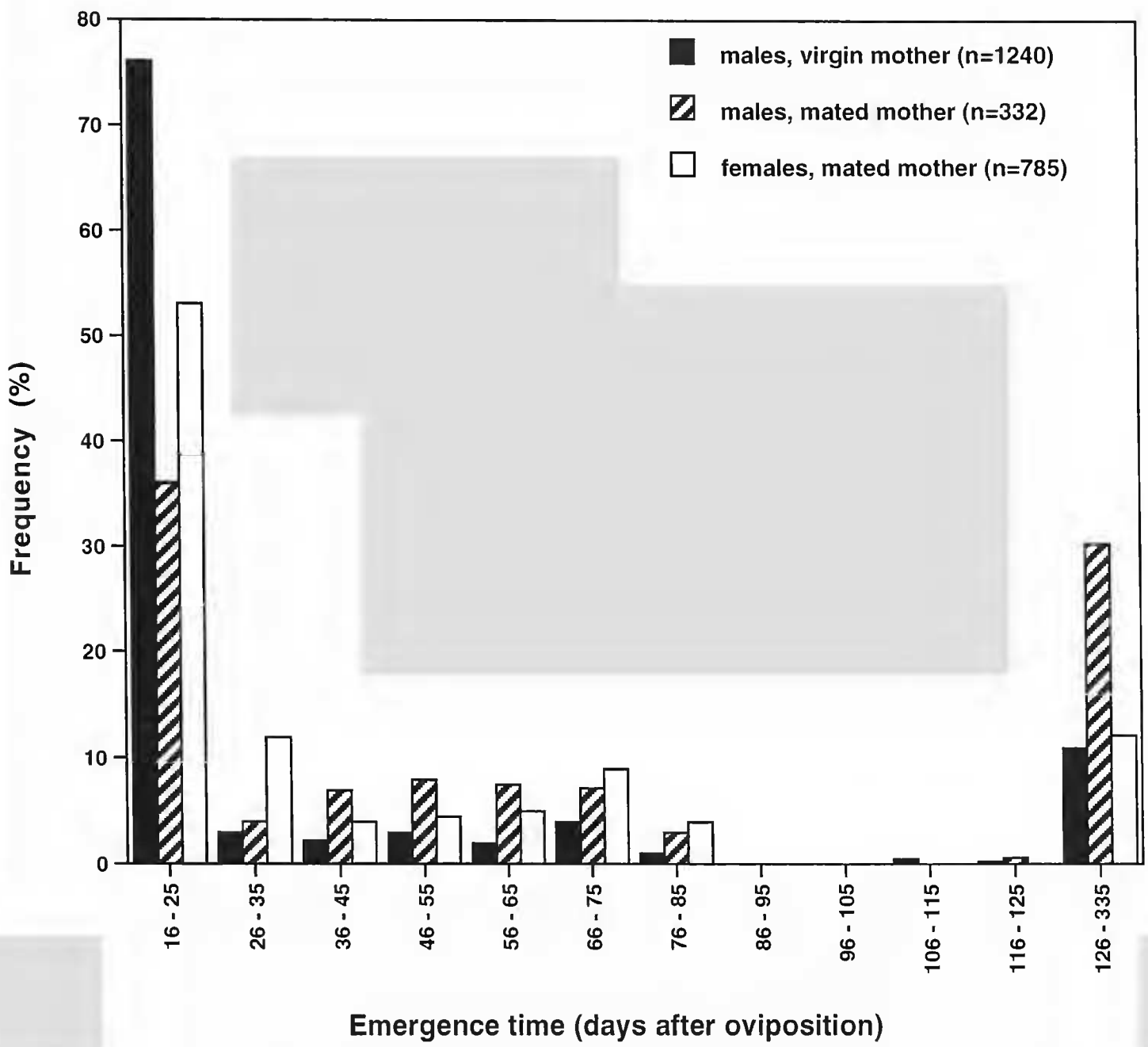

Figure 2. Frequency diagram to illustrate the temporal pattern of adult emergence in *Diachasmimorpha kraussii*, calculated from the time of oviposition of each individual. Data are presented separately by sex and according to the mating status of their mother.

was so in comparison with the males produced by virgin females (Kolmogorov-Smirnov two-sample test, $D_{(1240,332)} = 0.393$, $\chi^2 = 0.084$, $P < 0.05$). Specifically, many more of the males from virgin mothers emerged early (days 16–25), and relatively more males from mated mothers emerged late (126 days or more). The reason for this large disparity in emergence patterns between males produced by virgin and mated females is unclear, and we know of no other case of such a discrepancy in the literature. The analysis of cumulative emergence showed that male offspring in general took longer than their female siblings in achieving cumulative emergences of 50, 75 and 100% (Table 1).

Extended emergence by some brood members of opiine species has been recorded previously. In *D. longicaudata* cultured at 25° C, emergence time varied from 18 days to a year or more (Snowball et al. 1962, Clausen et al. 1965), which suggests that the staggered and protracted emergence times within broods ensures that at least some offspring of each female survives unfavourable conditions that might arise unpredictably.

Mated females produced significantly more females than males. The average sex ratio (± SE) of all offspring produced over the entire life of mated females was 0.28 (± 0.03, $n = 10$) (proportion males). The overall sex ratio of all progeny was 0.297 ($n = 1117$). Brood sex ratio was positively correlated with time of offspring emergence. Based on cumulative emergence, brood sex ratio increased with time (Pearson and Spearman Correlation Coefficients, $r = 0.85297$ and 0.90885, respectively, $P = 0.0001$).

Virgin females (50%, $n = 10$) also produced female offspring, but in very low numbers (1 female offspring/virgin female producing a female).

Diel Patterns of Emergence and Ovipositional Activity.—In the laboratory, most male and female wasps emerged during the first three to four hours after the lights came on and the number emerging gradually declined towards the end of the light period (Fig. 3). No wasps emerged during the scotophase (from 18:00 h to 06:00 h).

Under field conditions, both male and female wasps started to emerge from 0500h. The emergence rate gradually increased towards midmorning and declined in the afternoon (Fig. 4). No wasps emerged between 18:00 h and 05:00 h. Emergence times for parasitoids of both sexes under laboratory conditions were not significantly different from those recorded in the field (Kolmogorov-Smirnov two-sample test on data for males: $D_{(155,60)} = 0.252$, $\chi^2 = 10.988$, $P > 0.05$, and for females: $D_{(204,99)} = 0.208$, $\chi^2 = 11.535$, $P > 0.05$). The asynchronous pattern of adult emergence may be related to individual physiology.

We found no published records on the time of day that other opiine parasitoids emerge, but another braconid, *Bracon hebetor* Say, also emerged asynchronously under constant temperature and light intensity (Antolin & Strand 1992). Emergence time may not be constrained by strong natural selection, as these solitary braconids are not geared to mating at their natal site (see Antolin & Strand 1992, Rungrojwanich & Walter 1999), even though their hosts may be somewhat clumped, as in quasigregarious parasitoid species (Nadel & Luck 1992).

Mated female *D. kraussii* oviposited under both light and dark conditions in the laboratory (Table 2). The pattern of offspring production was influenced primarily by whether photophase or scotophase conditions prevailed (Tables 2 and 3). More than 60% of offspring were produced during the photophase, regardless

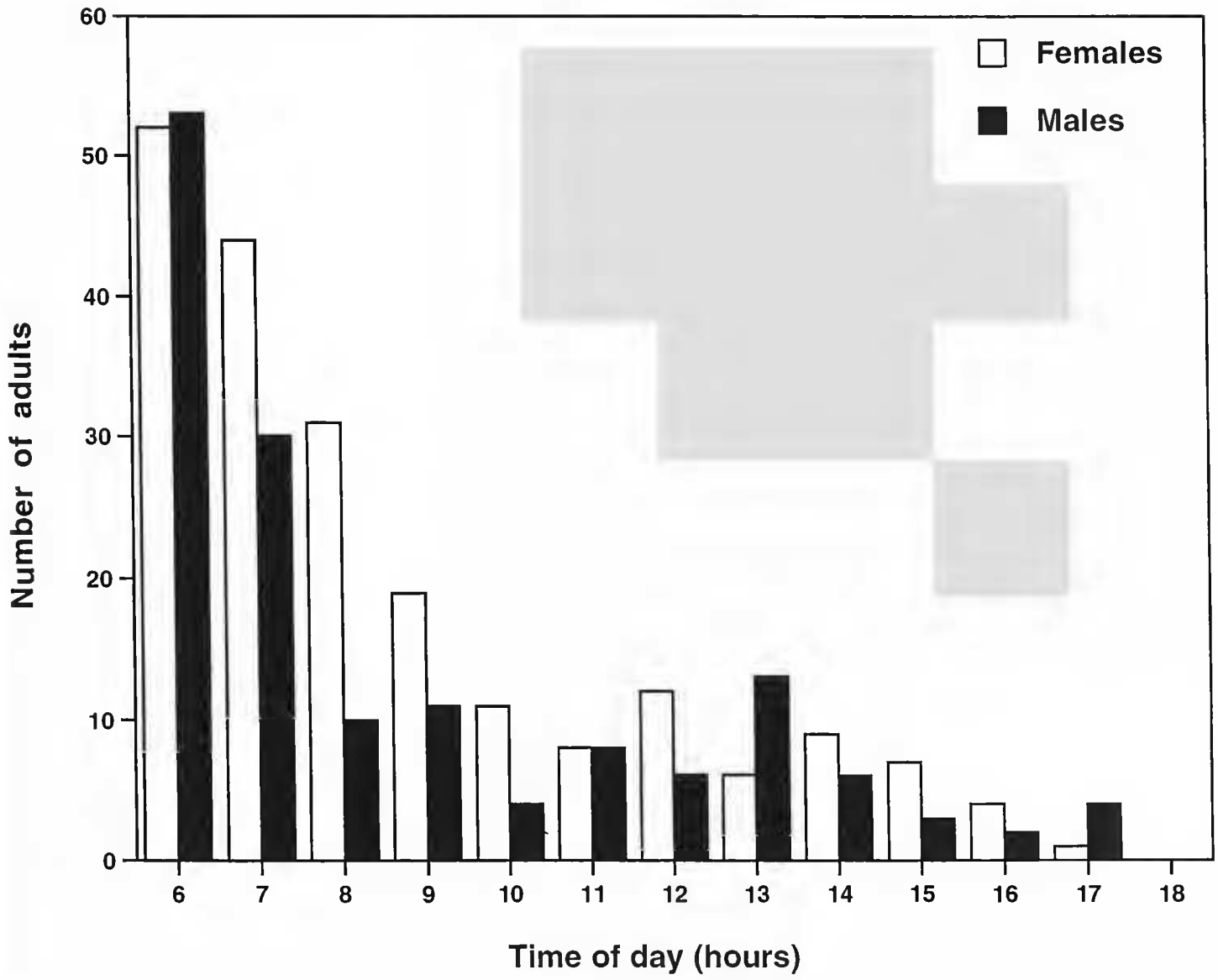

Figure 3. Total number of *Diachasmimorpha kraussii* that emerged hourly during the photophase under laboratory conditions.

of whether the parent females were exposed first to scotophase conditions or initially to photophase conditions.

The diel emergence data (Figs. 3 and 4) suggest *D. kraussii* is diurnal in the field, but the oviposition data suggests that oviposition may also take place at night, but at lower levels than in the day (Table 2). This has yet to be confirmed. Field evidence from other opiines is contradictory, but since most of it derives from light trapping, its implications for interpreting patterns of ovipositional activity are still unclear. Light traps, operated continuously for four years in Malaysia (1986–1989), attracted no fruit flies nor any opiine parasitoids (S. Vijaysegaran, personal communication), which does support our contention. Both sexes of another opiine, *Psyttalia incisi* (Silvestri), were attracted to a light trap set up in India, with most individuals caught between 19:00 h and 22:00 h (Banerjee 1989), so the species may be active nocturnally, or both nocturnally and diurnally. Different fruit fly parasitoid species may therefore respond differentially to light traps and may be active at different times of the day or night.

The only information on nocturnal oviposition by opiines in the field involves unquantified observations on *F. arisanus*. Females have been recorded ovipositing at night under laboratory conditions (van den Bosch & Haramoto 1951; G. M. Quimio, personal communication). *Fopius arisanus* females were seen ovipositing

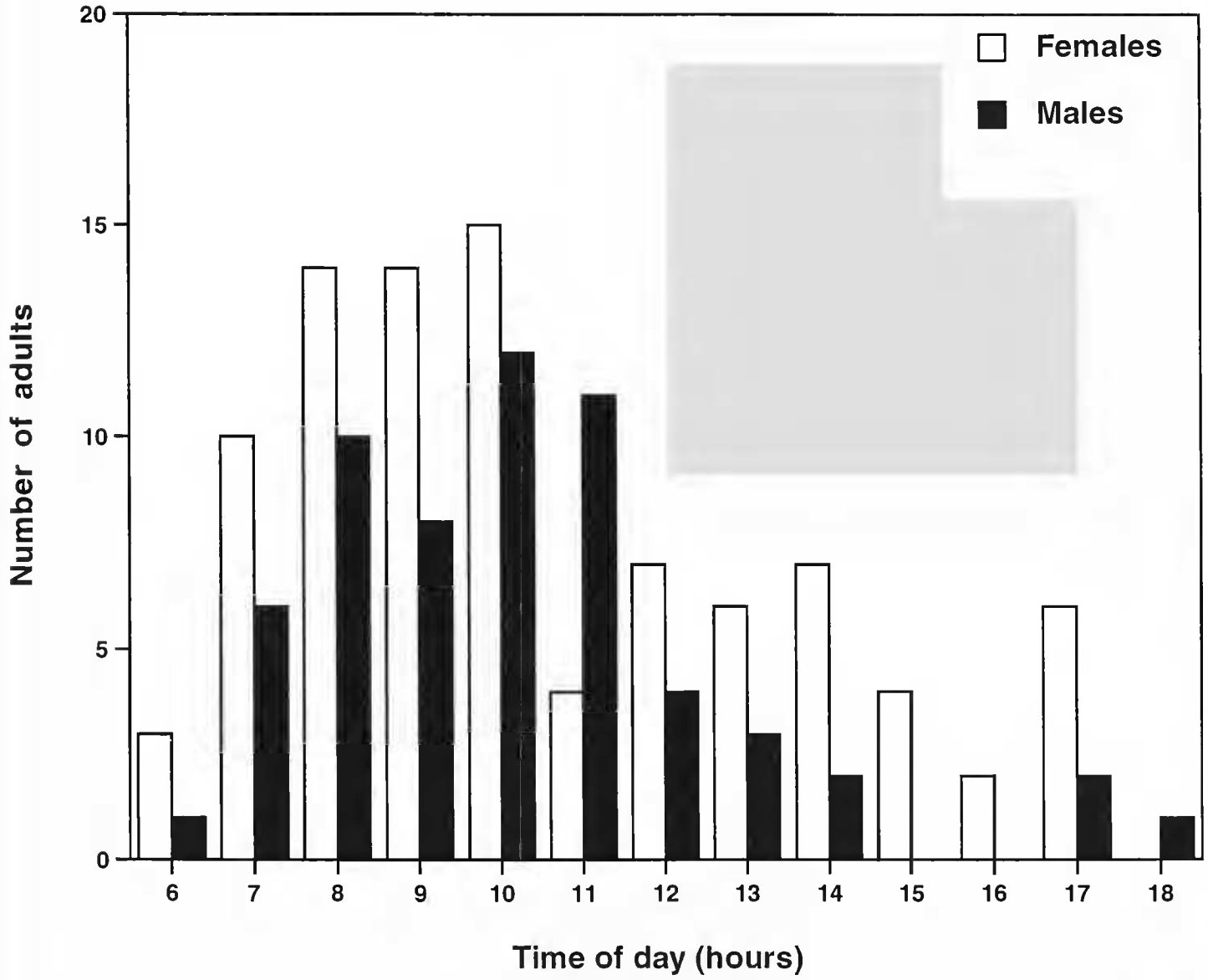

Figure 4. Total number of *Diachasmimorpha kraussii* that emerged hourly under field conditions.

Table 2. Numbers of adult offspring of *Diachasmimorpha kraussii* produced by six groups (= replicates) of mated *D. kraussii* females. The females in three of the groups were first presented with hosts during the photophase (labelled "photophase first") and the other three groups were first exposed to hosts during the scotophase ("scotophase first"). All wasps were exposed to new hosts at the change of the light phase, and this continued for three days.

		Photophase first		Scotophase first	
Rep	Day	Ph	Sc	Ph	Sc
1	1	37	25	48	15
	2	31	16	45	17
	3	34	16	39	18
2	1	27	15	39	27
	2	38	14	45	20
	3	26	19	38	21
3	1	25	27	28	14
	2	31	19	31	19
	3	28	20	24	15
Total		277	171	337	166
%		62	38	67	33

Table 3. Results of a three-way ANOVA testing the influence of day of exposure, light sequence (scotophase first treatment or photophase first treatment) and light conditions at the time of oviposition (scotophase or photophase). The test was performed on the untransformed raw data in Table 2. Transformation of the data did not affect the outcome.

Factors	df	Sum of squares	Mean square	F	*P*
Day (A)	2	45.167	22.583	0.635	0.5385
Light sequence (B)	1	84.028	84.028	2.363	0.1373
A × B	2	12.056	6.028	0.170	0.8451
Light condition (C)	1	2131.361	2131.361	59.945	<0.0001
A × C	2	70.056	35.028	0.985	0.3880
B × C	1	117.361	117.361	3.301	0.0818
A × B × C	2	29.389	14.694	0.413	0.6661

in the field during nocturnal observations on fruit fly activity (R. A. I. Drew, personal communication).

Australian Distribution, Host Flies and Host Plants.—Diachasmimorpha kraussii is distributed in the Northern Territory, Queensland and New South Wales (Fig. 5). There are no records further south than New South Wales although its best-known host, *B. tryoni*, occurs regularly in Victoria and sporadically in South Australia (White & Elson-Harris 1992). The list of host plants and fruit flies with

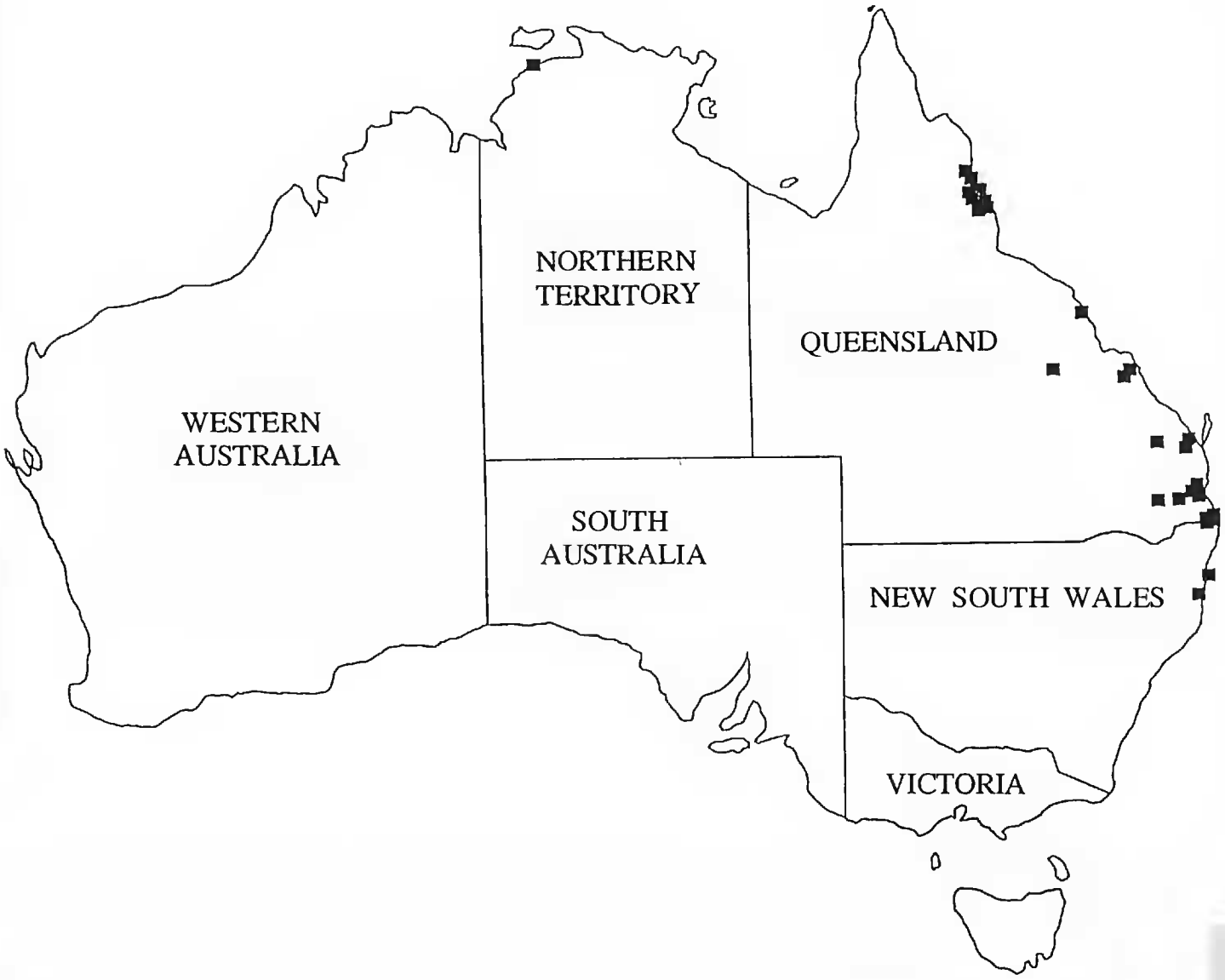

Figure 5. Distribution of *Diachasmimorpha kraussii* in Australia.

Table 4. List of host plants and host fruit flies (all in the genus *Bactrocera*) with which *Diachasmimorpha kraussii* has been associated. The number of records, from museum specimens, for each association is also given. The fly names are from the labels and all are still current (Norrbom 1998). Host plants and host fruit flies are not correlated across the table.

Host plant		Host fly	
Species	No. records	Species	No. records
Eugenia uniflora	regular*	*tryoni*	15; regular*
Psidium guajava	6	*jarvisi*	5
Solanum mauritianum	6	*neohumeralis*	3
Eriobotrya japonica	4	*cacuminata*	2
Mangifera indica	4	*aquilonis*	1
Terminalia catappa	4	*halfordiae*	1
Juglans regia	3	*kraussii*	1
Planchonia careya	3	*melas*	1
Prunus persica	2	*murrayi*	1
Solanum seaforthianum	2	*visenda*	1
Morus nigra	1		
Musa spp.	1		
Nauclea orientalis	1		
Persea gratissima	1		
Pyrus communis	1		
Terminalia melanocarpa	1		
Semecarpus australiensis	1		
Cherry guava	1		
Myer lemon	1		

* *Diachasmimorpha kraussii* was found in association with *Bactrocera tryoni* in *Eugenia uniflora* fruits regularly and in large numbers, when *E. uniflora* was fruiting in Brisbane (1991–1994).

which *D. kraussii* has been associated in the field is shown in Table 4 (which includes the records of May & Kleinschmidt (1954)). Six species of flies recorded here as hosts had not been listed by Clausen et al. (1965). The date and place of collection and the collectors are documented in full by Rungrojwanich (1994).

Acknowledgment

We thank Bob Wharton who kindly identified the parasitoid specimens. Sincere thanks for the kind favours of Eddie Hamacek who supplied us with fruit flies, Laurie Jessup who identified plant specimens, Joan Hendrikz, Laraine Law and Andrew Loch who advised on statistics and Tony Clarke, Jenny Beard and Stefan Schmidt who commented on the manuscript. The research was supported by an AusAID scholarship to K.R. and by the Department of Entomology, The University of Queensland.

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Received 29 Nov 1998; Accepted 10 Jul 1999.